

Predation by a carabid beetle specialized for catching Collembola¹⁾

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With 11 figures

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1. Introduction

Collembola are abundant in the litter layer and constitute food for most predatory arthropods (ERNSTING & JOOSSE 1974). The hemiedaphic species living on the soil surface are especially hard for active predators to catch because the action of their furca shoots them into the air within 20—50 ms when they are touched (BAUER & VÖLLENKLE 1976, CHRISTIAN 1979, BAUER 1982). Previous investigations have shown that predators use very different hunting strategies to overcome this rapid response. The diurnal ground beetle *Notiophilus biguttatus* (FABRICIUS, 1779) for example has well developed compound eyes which it uses to gauge accurately the position and distance of a springtail before it attacks (BAUER 1981). In the larvae of the same species, however, visual orientation is of no importance in predatory behaviour but they detect aggregations of Collembola by means of chemical cues. The attack is triggered and directed when the trichobothria of the head make contact with a springtail. This contact is too gentle to elicit the escape response (BAUER 1982).

Investigations of the crop contents have revealed that only few carabid species can be regarded as specialized Collembola predator (HENGEVELD 1980), among them *Loricera pilicornis* (FABRICIUS, 1775). This holarctic species is hygrophilous and lives on soft, shaded soil at the border of fresh, usually standing water (LINDROTH 1961). It belongs to the phylogenetically isolated tribe Loricerini, all of which are characterized by the strikingly thickened 4 proximal segments of the antenna bearing very long, erect setae (Fig. 1). There is also a dense arrangement of long setae on the ventral side of the head (Fig. 2, 7). *L. pilicornis* has strongly convex eyes and reacts to moving prey with turning movements typical of insects hunting by sight (cf. HORRIDGE 1977). However, unlike other Carabidae hunting visually (e.g. *Notiophilus* sp., *Elaphrus* sp., *Asaphidion* sp.), *Loricera* is able to catch Collembola in total darkness too. Under experimental conditions more than 70% of the attacks on a species of collembolan (*Heteromurus nitidus* TEMPLETON, 1835) were successful, more than in any other species so far tested (cf. BAUER *et al.* 1977).

It is likely that, in addition to the eyes, the unique structure of the antennae and the unusual array of setae on the head and antennae are important for the hunting behaviour of the species.

This paper investigates how *L. pilicornis* detects its prey and overcomes the escape mechanism of springtails.

2. Material and methods

The beetles were caught in the spring in moist shady places by the Danube in Bavaria, Germany (GFR). They were kept on moist plaster of Paris and fed with *Heteromurus nitidus* (Collembola) from a laboratory culture kept on moist plaster and fed with soya flakes.

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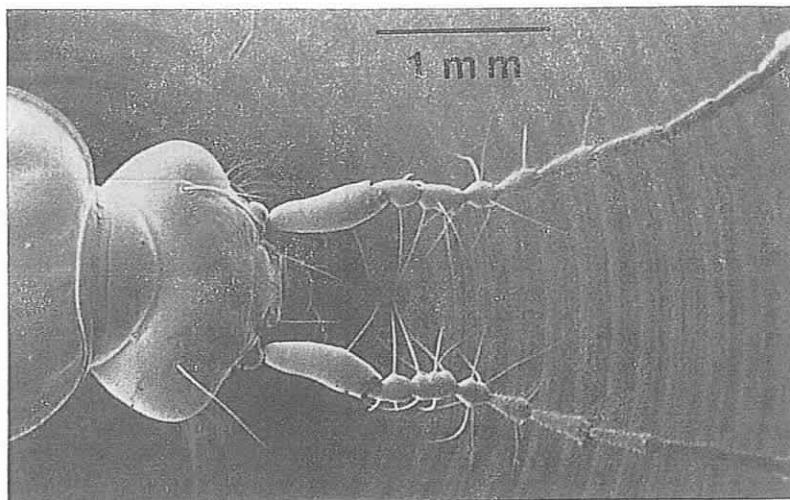


Fig. 1. *Loricera pilicornis*: Head and antennae bearing setae from above.

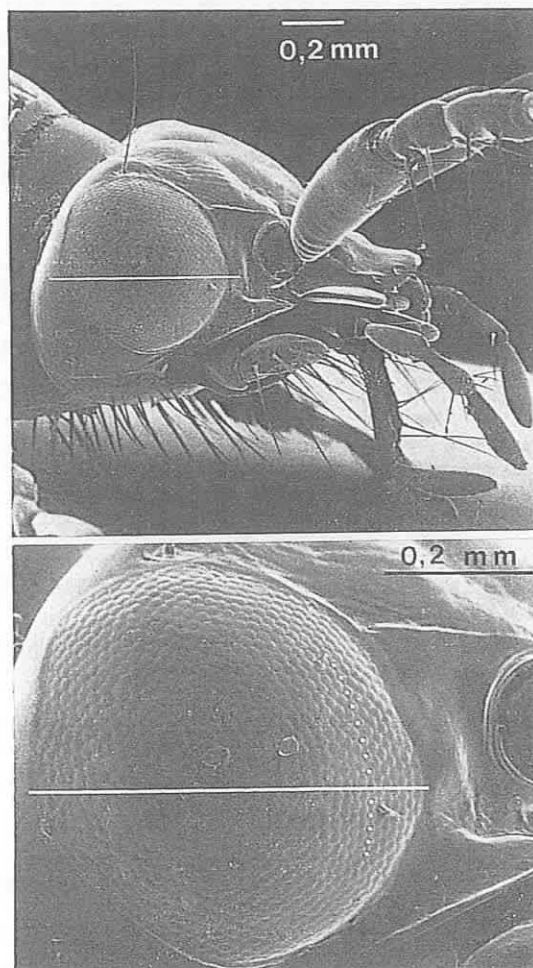


Fig. 2. Head and compound eye of *Loricera pilicornis*. The white line indicates the horizontal plane; white marks: 7th y-row of ommatidia.

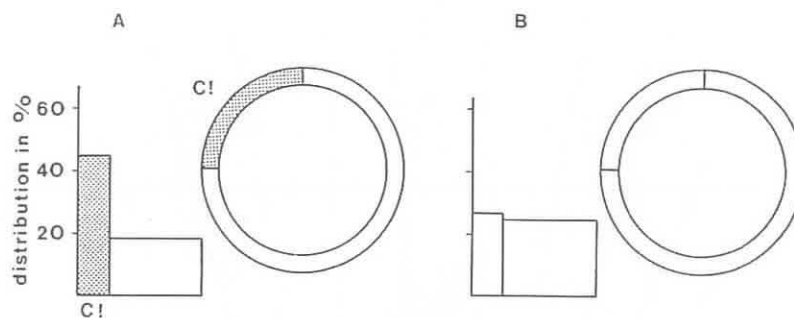


Fig. 3. Distribution of the beetles in the ring-shaped channel. A: One quarter of the channel contaminated (C!) by Collembola; B: Control experiment, uncontaminated.

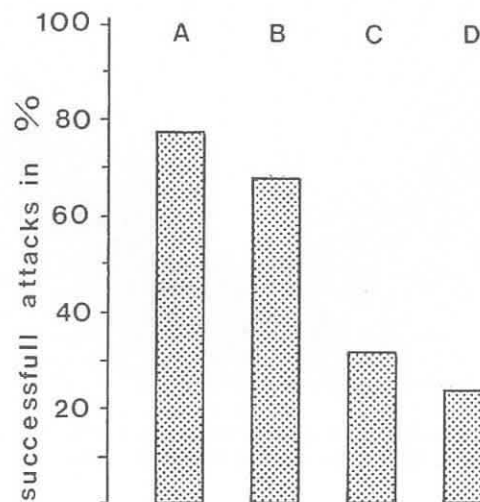


Fig. 4. Rate of capture by intact and operated beetles. A: intact: 217 attacks by 36 beetles were observed; B: eyes covered, 217 attacks/11 beetles; C: antennal setae shortened, 368 attacks/17 beetles; D: setae of antennae and head shortened, 468 attacks/16 beetles. Difference between A and B significant at $p < 0.02$, between A and C at $p < 0.001$, between C and D at $p < 0.02$ (χ^2 -Test, cf. Rasch 1970).

Chemical orientation: A ring-shaped channel (radius 10 cm, annular width 2 cm, height 0.6 cm), open at the top, with a floor of moist plaster was divided into four sectors of equal size. Strips of plasticine embedded in the plaster floor prevented chemicals diffusing between the sectors. A population of 50 *Heteromurus nitidus* was confined in one of the four sectors. After 5 days the spring-tails were removed and the area was cleaned with a blast of air. Beetles, starved for 4 days, were then introduced singly into the channel and observed for 10 minutes. The control experiment was carried out in the same way except that the plaster floor was uncontaminated. Experiments were run in red light with the light source above the centre of the apparatus. To avoid any other directional stimuli which might influence the distribution of the beetles (e. g. magnetic field, inhomogeneity of the light through polarization etc.), the apparatus was turned 45° after each beetle was tested.

Elimination of vision: The beetles were narcotized with CO_2 and their eyes covered with a mixture of shellac and soot. 2–3 hours after this procedure they were confronted with Collembola. The eye covers were inspected after each experiment because the beetles tried to slip them off. Only results from beetles with intact covers were considered.

Removal of the setae: The beetles were narcotized and fixed on a block of wax. The setae were cut off carefully under a binocular microscope using tweezers with ground tips. With this procedure it was possible to shorten the setae to approximately a quarter of their entire length.

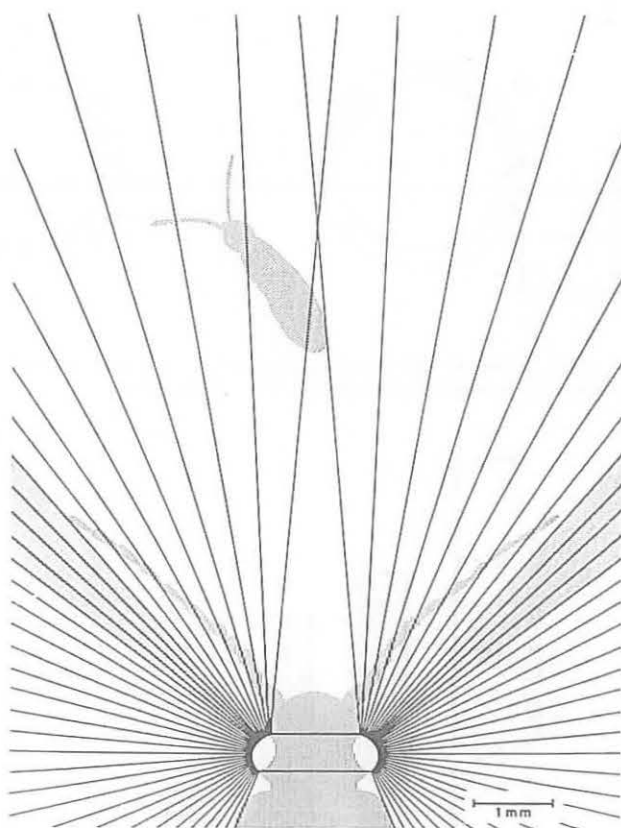


Fig. 5. The field of view of *L. pilicornis* in the horizontal plane with a springtail in view. The stippled area marks the foveal region with interommatidial angles of $< 3^\circ$. The medial visual cones do not overlap completely.

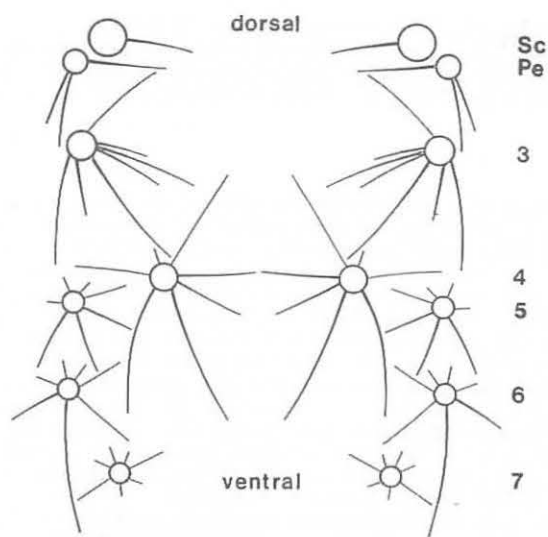


Fig. 6. Scheme of size and direction of the setae on the proximal antennal segments shown diagrammatically as a series of transversal sections seen from the front. Sc: Scapus; Pe: Pedicellus; 3—7: antennal segments. Scale line: 1 mm.

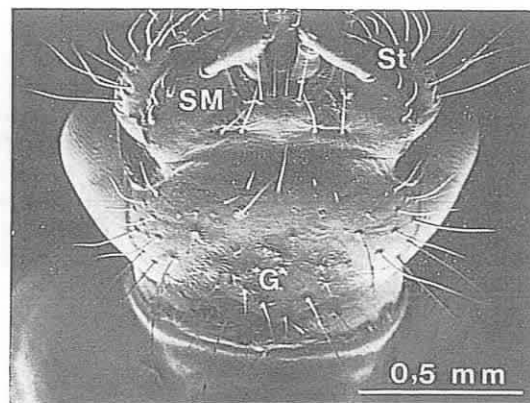


Fig. 7. The ventral surface of the head to show the arrangement of setae; G: Gula, SM: Submentum, St: Stipes.

Structure of the field of view: The horizontal plane of the eyes (cf. Fig. 2) was revealed from films of the beetles' hunting behaviour which were taken exactly from the side. Living beetles were fixed in plasticine and mounted on a goniometer under a binocular microscope (Zeiss Opmi). The direction of view of the ommatidia in the median horizontal plane was determined by using the deep pseudopupil (cf. STAVENGA 1979), which in bright coaxial light can be seen as a small black spot within the principal pseudopupil.

Starting with the eyes in a symmetrical position, the beetle was turned in the horizontal plane to the left and to the right in steps of 3° . After each turn the number of y-rows from the inner margin of the eye to the position of the deep pseudopupil was counted (for further details of the pseudopupil method see HORRIDGE 1978). Finally the mean values from the eyes of 4 beetles were used. The optical axes of the ommatidia were drawn on the contour of a section of the same plane through the head.

Performance of intact and operated beetles in capturing springtails: Collembola (*Heteromurus nilidus*) of equal length (1.3 mm) were sorted from the culture population by using gauze sieves of different mesh size. Single beetles were confronted with 3 Collembola in a circular vessel (radius 8 cm, height 12 cm) with a bottom of blackened moist plaster. The sides of the vessel were covered with black paper to a height of 3 cm above the bottom so that the yellowish coloured Collembola were clearly visible against the black background (contrast approx. 0.76, cf. BAUER *et al.* 1977). The vessel was illuminated by two lamps, one on each side. Its surface was covered with greaseproof paper apart from an observation aperture in the lid in order to get diffuse light at the bottom and to avoid disturbing the beetles by movements of the observer. The light intensity at the bottom of the container was 150 lx. Three to fifteen attacks by each beetle were observed and success or failure recorded.

High speed photography: A total of 39 attacks of *L. pilicornis* was filmed at rates of 500–1050 frames per second, using a Hycam camera with a Strobokin flash lamp (Impulsphysik, Hamburg) as the light source. The recordings were made in the Institut für Wissenschaftlichen Film (IWF), Göttingen, Germany (GFR).

Recordings from the side: A beetle and a springtail were enclosed in a narrow cuvette (length 40 mm, width 6 mm, height 40 mm) but separated from each other by a piece of metal of the same width. The barrier was removed and the camera was triggered when the two animals approached each other. In order to get sufficient light intensity the cuvette was illuminated from behind, so that the beetle and its prey were seen in silhouette. Recordings from above: In this case the cuvette had a ground space of 2×3 cm. The base consisted of frosted glass and was illuminated from below.

3. Results

3.1. Chemical orientation

Collembola are abundant in the litter layer but they are not distributed homogeneously over the floor. In dry conditions and during moulting and reproduction, springtails aggregate in moist places (for literature see VERHOEF & NAGELKERKE 1977). These aggregation sites are marked by species-specific aggregation pheromones (for literature see JOOSSE & KOELMAN 1979). The probability of a predator encountering Collembola would be increased if it could locate the aggregation sites by means of chemical cues and select habitats where the prey is abundant.

The beetles were placed in the channel at the side opposite to the contaminated sector. The time was recorded from the moment when the beetle crossed the sector border. The majority of them immediately showed a searching behaviour with rapid movements of the antennae. The 30 beetles observed in this experiment spent 44.46% of their time in the contaminated sector (Fig. 3) (mean value 4.45 min, S.D. $\pm$ 1.58). In the control experiment, when the same sector was uncontaminated the beetles stayed there for 26.79% of the time (mean value 2.68 min, S.D. $\pm$ 1.12). The difference between the experimental and control results is significant ($p < 0.001$, Welch test, BROWNLEE 1965). This indicates that *L. pilicornis* is able to detect sites where Collembola are abundant by means of chemical cues.

3.2. Hunting behaviour and hunting success of intact and operated beetles

If a hungry *L. pilicornis* detects a moving springtail by visual cues it turns towards the prey, immediately jumps forward and attempts to seize the prey. This behaviour is different from that of other ground beetles hunting by sight which make jerky approaches before attacking and the actual capture is made at a critical distance (cf. BAUER 1981). It was therefore predicted on the basis of these observations, that 1) *L. pilicornis* is unable to estimate the distance of the prey visually and 2) that the accurate location of a springtail before the attack is not as crucial for success in hunting as in other species. This assumption was confirmed by testing the hunting ability of beetles with covered eyes. They were less active than intact beetles and unable to perceive moving prey at a distance. But when they accidentally touched a springtail with the antennae they immediately struck in the direction of contact and 67.7% of the attacks were successful, compared with 77.1% in intact beetles (Fig. 4). The shortening of the setae on the 4 proximal antennal segments reduced the rate of capture to 31.5%. When the setae on the ventral side of the head were also shortened only 23.9% of the attacks were successful. These results confirm the assumption that these setae are important for predatory behaviour in this species.

3.3. The field of view of the eyes and the setae

The number of ommatidia in the corneae of 6 beetles averaged 807 (S.D. $\pm$ 44.1). With the head in its normal position, the horizontal plane cuts through the middle of the eyes below the base of the antennae (Fig. 2). In this plane the medial margin of the eyes projects furthest anteriorly and medially. This is different from other ground beetles which hunt visually, where the antennae are always inserted beneath the inner margin of the eyes. In *L. pilicornis*, however, the frontal field of vision is directed anteriorly under the antennae.

The picture of the visual field in the horizontal plane (Fig. 5) indicates two other differences from typical species hunting by sight: 1) there is no complete binocular overlap, not even in the visual cones of the ommatidia at the medial margin of the eyes; 2) *L. pilicornis* has a fovea, an area containing ommatidia with the narrowest angles ($< 3^\circ$), but this looks fronto-laterally, rather than straight ahead.

There are 27 enlarged setae on the proximal segments of the antennae, mainly directed medially and ventrally (Fig. 6). From the 5th segment onward they become increasingly more terminal and radial in position, as they are in the antennae of other Carabid species. On the ventral head surface are 98 setae, 52 on the gula, 16 on the praementum, 22 on the stipes and 8 on the basal parts of the maxillary palps. They differ in length between 100—800 μ m, with the longest situated marginally (cf. Fig. 7).

3.4. The attack

The high speed film revealed details of hunting behaviour. When *L. pilicornis* recognizes a springtail (either visually or by antennal contact), it moves rapidly towards it, accelerating jerkily over the last 2—4 mm. This acceleration takes approximately 30 ms ($n = 27$, S.D. $\pm$ 6.8). At the beginning of the forward movement, the antennae are opened out at approxi-

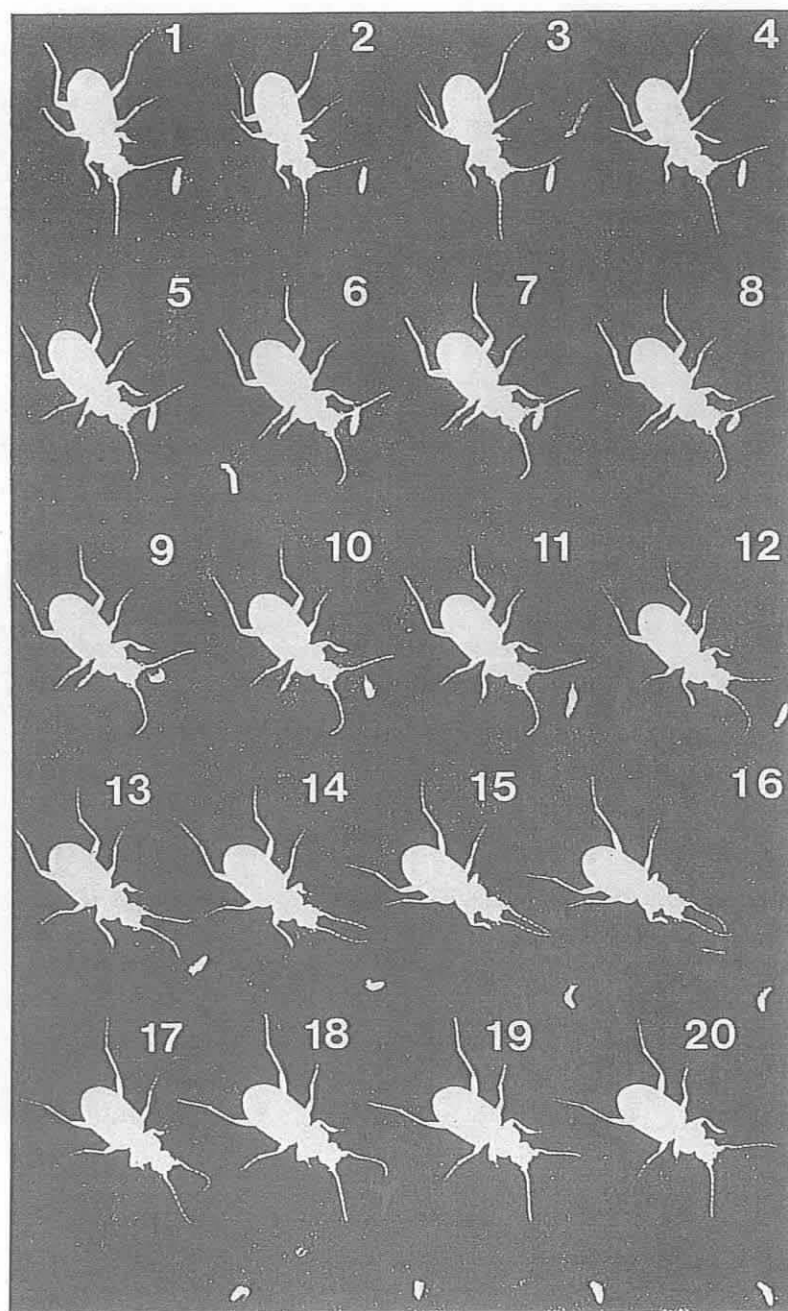


Fig. 8. A failed attack of *L. pilicornis*. 1—7: antennal contact with the springtail, 8: the springtail jumps, 12—15: the beetle strikes the antennae together (too late), 16—20: the antennae are reopened. Single frames from a film recording at 500 frames/s. The beetle is 7 mm long.

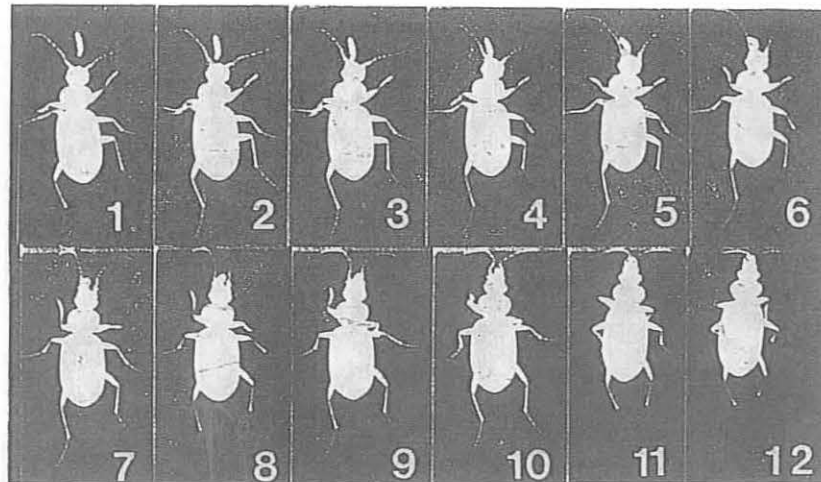


Fig. 9. Successful attack. 5: the springtail tries to jump, 6—12: the beetle hurls its body forward and strikes the antennae together (500 frames/s).

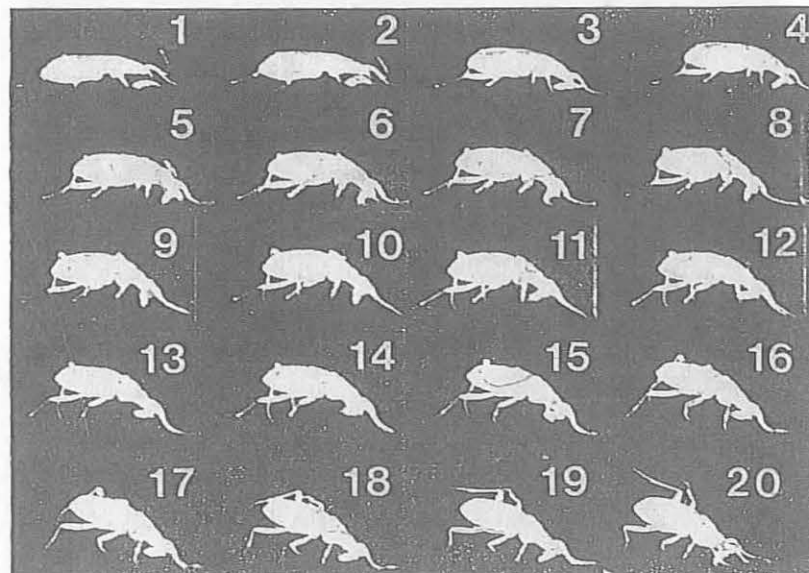


Fig. 10. Successful attack, seen from the side, 1: the springtail under the head of the beetle; 3: the beetle grasps it; 4—12: the springtail shoots out its furca and raises the beetle; 13—20: the springtail is pressed down (500 frames/s).

mately 40° from the midline and the prey is swept along by the ventrally directed setae if it is not exactly in front of the head. If the springtail gets underneath its head, the beetle strikes the proximal segments of the antennae together within 12 ms ($n = 14$, S.D. ± 3.46 ms) (cf. Fig. 8, 9), so that the medio-ventrally oriented setae prevent the springtail from escaping forward, upward and to the sides. Antennal closing is probably released by the prey contacting the palps. Simultaneously the head is pressed down and the springtail, fenced in by the setae on the ventral surface of the head, is grasped with the beetle's mouthparts (Fig. 10). If the attack fails, the beetle tries again. The shortest space of time between antennal closings was 64 ms. During seeking behaviour after a failure, fast turning movements of up to 26.56 rad/s can be observed.

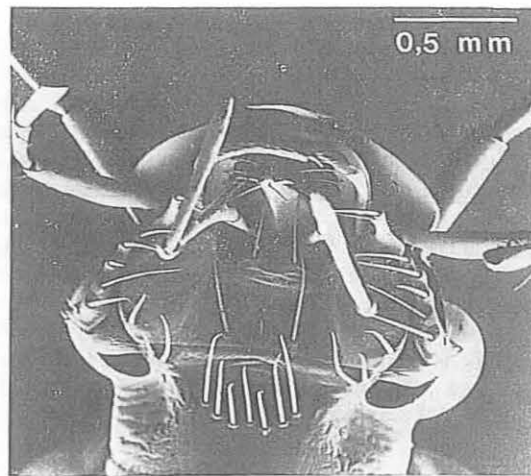


Fig. 11. *Leistus rufimarginatus* DUFTECHMID, 1812: Ventral surface of the head, showing the cavity surrounded by large setae.

4. Discussion

Carabid beetles are primarily carnivorous (for exceptions see THIELE 1977) and generally feed on all animals they are able to overcome. Among 24 species of 13 genera HENGVELD (1980) found 3 genera which seem to be specialized to feed on Collembola: *Notiophilus*, *Leistus* and *Loricera*.

The *Notiophilus* species with their well developed compound eyes are typical of visual hunters (BAUER 1974): they are exclusively active by day (THIELE 1977) and hunt their prey on the soil surface by means of visual cues (SCHALLER 1949, BAUER 1981). The fact that their crop contents consist to a great amount of Collembola (DAVIES 1953, ANDERSON 1972, HENGVELD 1980) may be due to the great abundance of springtails in the litter layer. On the other hand the accuracy with which this genus gauges distance and position of a springtail visually before the attack (cf. BAUER 1981) can be regarded as a specialization for hunting prey which reacts rapidly and has a high speed escape mechanism.

The hunting behaviour of *Leistus* sp. is completely unknown. These species have strongly convex but not very large eyes and seem to be active in the dark (LUFF 1978, DEN BOER 1979). The setal equipment of the antennae is similar to that of other Carabidae but on the ventral surface of the head is a cavity bounded by a circle of centrally directed setae well suited to prevent a springtail from escaping when it gets under the head (Fig. 11).

The 15 species of the holarctic tribe Loricierini are characterized by the unusual shape of their antennae and by the length of the setae. In *L. pilicornis* and probably also in the other species this equipment occurs with an antennal strike mechanism, unique in insects, used for attacking its prey.

The sensory equipment and predatory behaviour of *L. pilicornis* are well adapted to its ecological niche. The beetles are abundant and widely dispersed (DEN BOER 1977) but they are hygrophilous and therefore restricted to moist shaded soil. In such sites the high water content of the soil forces the Collembola to stay on the surface, where they often cluster. *L. pilicornis* is able to detect aggregations of its prey by chemical cues. If it attacks such an aggregation the antennal setae may sweep several springtails under the head simultaneously and enhance the chance to grasp one of them.

The antennal strike too may have evolved under the conditions on bare wet soil. It is unlikely to be so successful in the cavities of the litter layer where antennal movements are confined. *Notiophilus biguttatus* on the other hand is a good example of an inhabitant of the litter layer in woodlands: it folds the antennae back at an angle shortly before it reaches critical attacking distance (BAUER 1981).

L. pilicornis has no fixed daily activity pattern. The beetles are active both in the dark and during the day (THIELE & WEBER 1968, LUFF 1978). This accords with the beetles' ability to use visual cues in their predatory behaviour although they are not dependent on them as are the typical diurnal species which hunt visually (BAUER *et al.* 1977).

With respect to its field of view, *L. pilicornis* seems to be intermediate between typical visual hunters and nocturnal Carabidae: it has fewer ommatidia than diurnal species. Like the visual hunters it has a fovea but this is directed antero-laterally rather than anteriorly. It has spherically enlarged compound eyes but no binocular overlap. *L. pilicornis* is able to perceive the direction of a moving prey animal, but it obviously cannot estimate its distance by means of visual cues (for the problem of distance estimation by compound eyes see WEHNER 1981). This deficiency, however, is compensated by the dense array of enlarged setae and the antennal strike which cooperate as a kind of trap during the attack.

Further investigations of the hunting behaviour of soil arthropods will probably reveal other sophisticated ways of overcoming the high speed escape mechanism of springtails.

5. Zusammenfassung

(Beutefang bei einem auf Collembolen spezialisierten Laufkäfer)

Der holarktische Carabide *Loricera pilicornis* lebt auf feuchten, schattigen Böden und ernährt sich hauptsächlich von Collembolen der Bodenoberfläche. Die Käfer können Aggregationen ihrer Beute chemisch wahrnehmen (Fig. 3). Auf bewegte Beute reagieren sie mit den für visuell jagende Insekten typischen Wendebewegungen. Ihre Sehrammstruktur unterscheidet sich von der typischer visuell jagender Arten durch das Fehlen der binokularen Überlappung und dadurch, daß die Fovea nach vorn-lateral anstatt nach vorn gerichtet ist. Das Sehvermögen ist für den Fang Erfolg weniger wichtig als die vergrößerten Borsten auf den basalen Antennengliedern und auf der Ventralseite des Kopfes (Fig. 1, 2). Schwärzung der Augen reduzierte die Fangrate von 77 % (intakte Käfer) auf 68 %, Kürzung der Borsten auf 24 % (Fig. 4). Hochfrequenzaufnahmen des Fangverhaltens ergaben, daß die borstentragenden Segmente der Antennen in der Endphase des Zugriffs in 12 ms zusammengeschlagen werden, wodurch die Collembolen mit den Borsten eingeschlossen und am Entkommen gehindert werden (Fig. 8, 9, 10). Die Zusammenhänge zwischen Fangverhalten und sensorischer Ausstattung der Käfer und ihrer ökologischen Nische werden diskutiert.

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Synopsis: *Original scientific paper*

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The holarctic ground beetle *Loricera pilicornis* (Coleoptera, Carabidae) lives on shaded moist soil and feeds mainly on surface inhabiting Collembola (springtails). The beetles are able to detect aggregations of their prey using chemical cues. They react to moving prey with turning movements typical of insects hunting by sight. The arrangement of their fields of vision differs from that of typical visually hunting Carabidae in that they have no binocular overlap and the fovea is directed fronto-laterally rather than frontally. Vision is not as crucial for the hunting success as the enlarged setae on the basal antennal segments and the ventral surface of the head. Blackening of the eyes reduced the capture rate from 77% (intact beetles) to 68%, shortening of the setae to 24%. High speed films of the final phase of the hunting behaviour revealed that the basal antennal segments, which carry the setae, strike together within 12 ms so that the setal array encloses the springtail and prevents it from escaping.

The relations between hunting behaviour, sensory equipment and ecological niche of *L. pilicornis* are discussed.

Key words: Carabidae, Collembola, predation, compound eyes, field of vision, antennal strike.